4. On the Structure and Function of the Mouth-parts of the Palæmonid Prawns. By L. A. BORRADAILE, M.A., F.Z.S., Lecturer in Zoology in the University of Cambridge, Fellow, Dean, and Lecturer of Selwyn College.

(Text-figures 1–51.)

I.

In the course of an investigation of the commensal prawns of the subfamily Pontoniinæ, it became necessary for me to compare their mouth-parts with those of the free-living Palæmoniinæ, in order to discover whether there existed between these groups any difference, in the organs in question, which might correspond with the difference in the diet of the animals. For the most part I have taken as representative of the Palæmoninæ the Common Prawn (*Leander serratus*), in which I have studied in some detail the structure and arrangement of the mouth-parts, and endeavoured, by the observation of living specimens, to find out how the organs in question are used. Surprisingly little trace has appeared of such structural differences between the subfamilies as I was looking for, but my observations have suggested, with regard to the morphology and functions of the parts around the mouth of Palæmonidæ, certain reflections and conclusions which form the subject of this communication.

II.

1. The morphology of the jaws of Malacostraca is still in a good deal of confusion, and there is much disagreement as to the relation of the parts of each of them to those of other crustacean limbs, and even as to the names to be applied to certain of their processes or "laciniæ"*. A great part of this difficulty arises from the fact that no theory as to the primary form of limb of which all the appendages of Crustacea are modified representatives has met with general acceptance. This thorny question is not

---

* I have not, in this summary article, made any reference to the literature of the subject. The contributions of Beecher, Boas, Claus, Coutière, Hansen, Huxley, Lankester, Packard, Thiele, and others to our knowledge of homology of the limbs of Crustacea are well known to those who are interested in the subject. The reader will readily gather in what respects my views differ from or agree with those expressed by each of them, and it is needless to emphasize the fact that all present speculation must be based upon the foundation they have laid.

only raised by the jaws of Malacostraca, but receives from the study of some of them—notably from that of the maxilla—considerable elucidation. The following, briefly stated, are the considerations in regard to it which have influenced the morphological suggestions put forward in the present paper.

2. It is not to be assumed without question that a prototype can be found from which all the limbs of all Crustacea can be derived by modification. The mere fact that appendages stand in the same position on the bodies of two or more segmented animals, or are members of the same meristic series in one animal, affords no ground for the assumption that there exists a common plan which underlies the arrangement of the parts of each of them. Moreover, even when there are resemblances between them, such a conception as that of a common type of them is of no use to the zoologist unless the plan of the type does not merely exist in the imagination of the observer, but has or at some time had an objective existence as a factor in development. Resemblances between two limbs may be due either solely to extrinsic causes—that is, to influences from without the organisms, which have brought it about that different developmental processes result in similar structures in the two cases,—or also to intrinsic causes—that is, to the operation of identical developmental factors. Only in the latter case has a common plan for the two limbs an objective existence. Conceivably such a plan may not be due to community of ancestry in all instances. When two appendages closely resemble one another—as do, for instance, the various antenniform limbs of Arthropoda—it is possible, and sometimes probable, that there exist in the mechanism of development facilities for establishing such organs, and that these have come into play independently more than once, forming appendages upon the same plan. This principle, however, is of limited application. Even in the cases which suggest it, it can never be applied save to actual features which exist in all the limbs under comparison. To assume the existence of a plan *of which some features are not realized* in each limb is quite unjustified, except on the hypothesis of the common inheritance both of a type of limb and, in the case of serial resemblance, of community of type between the members of the series of limbs [*]. To look for traces of a common type in structures in which it is so little obvious as in the appendages which appear to correspond in different Crustacea would be absurd, unless there were grounds for believing that their possessors were descended from a common ancestor; and if we are also to find community of type between the several limbs of each individual crustacean, then such community must have existed among the appendages of the ancestor.

---

[*] The resemblances here classed as due to extrinsic causes are those which are generally classed under the head of Analogy. Those which are due to common descent are instances of Homology. Those which are due to independent operations of the same developmental facilities (if such there be) form a third class not strictly the same as either Analogy or Homology.

For if (as might well be, by homœosis) it were independently established in any members of the subphylum, then the altered limbs would lose what they had in common with the corresponding limbs of other Crustacea.

3. In point of fact, however, there can be no doubt that the Crustacea are monophyletic, and it is very highly probable that their ancestor possessed a complete series of similar limbs. The widest gaps in the crustacean system are those which separate the Copepoda and the Cirripedia from the rest of the subphylum, but it is quite impossible even in these cases to entertain the suggestion of an independent origin. The occurrence of the nauplius would by itself negative this. That in the common ancestor of the group all the limbs, with the possible exception of the antennules, conformed to one type may be gathered with some confidence from the conditions in Branchiopoda and Trilobita. The Branchiopoda are certainly the most primitive of existing Crustacea. They alone possess in a simple form—allowance being made for certain obvious specializations, such as the degeneration of the mouth-parts—all the elements of the organization of every other class of the subphylum, and their suggestive resemblances to the Annelida are the only indications of affinity with other phyla shown by any recent members of the group. These facts fairly entitle them to be regarded as indicating broadly the ancestral features of the Crustacea. It is needless to dwell upon the fact that their trunk-limbs are all of one type, and, although that type becomes unrecognizable in their maxillæ and maxillules, its presence in these limbs of other groups (Ostracoda, Malacostraca, and Copepoda) supplies the lacking evidence here. In the Trilobita, which are without doubt related to the forbears of the Branchiopoda, a single type of limb extends throughout the body, from the antennæ backwards. It is not possible to avoid attributing to the ancestor of the Crustacea that similarity of appendages which characterizes these groups. This, of course, is not to say that the limbs of the first crustacean resembled closely either those of the Trilobita or those of the Branchiopoda. The form of the primitive crustacean appendage can only be conjectured with probability after comparison of all those which may be assumed to be derived from it. But, whatever it may have been, the foregoing considerations justify the belief that it existed, and that from it can be derived all the post-antennular limbs of every member of the subphylum.

4. The primitive limb of the Crustacea must have been of the kind to which the terms "leaf-like" and "phyllopod" are applied—that is, flattened, lobed, and feebly, if at all, jointed (text-fig. 2). This is à priori likely in view of the structure of the parapodia of Annelida, and seems established by the way in which the phyllopod limb is distributed among the Crustacea, occurring as it does throughout the trunk of Branchiopoda (text-figs. 3–5), on the hinder and presumably less mature, segments of *Triarthrus* (text-fig. 6), in Leptostraca (on the thorax,

text-fig. 8), and in the hinder part of the head of all groups. Whether it was biramous, like most parapodia, the limbs of the Trilobita *, and many of those of the higher Crustacea, is another question. In the majority of biramous crustacean limbs the
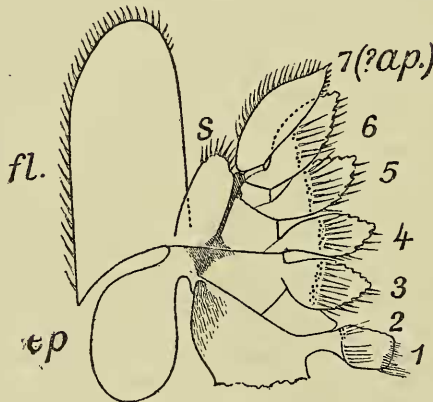
Text-figure 1.   Text-figure 2.
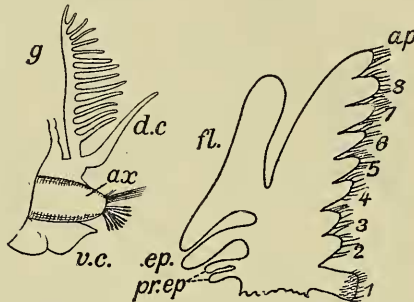
Parapodium of *Eunice maxima*,   Hypothetical limb of
after Ehlers.   proto-phyllopod.

For lettering see p. 71.

Text-figure 3.

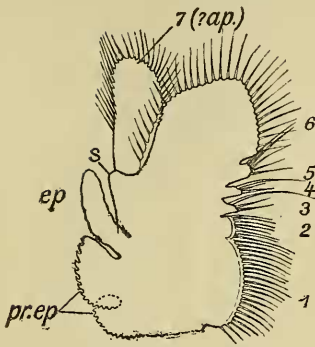Tenth thoracic limb of *Apus* sp.
For lettering see p. 71.

protopodite and endopodite form an axis to which the exopodite is appended, while the trunk-limb of the Branchiopoda is so clearly uniramous that there is discussion as to which of its
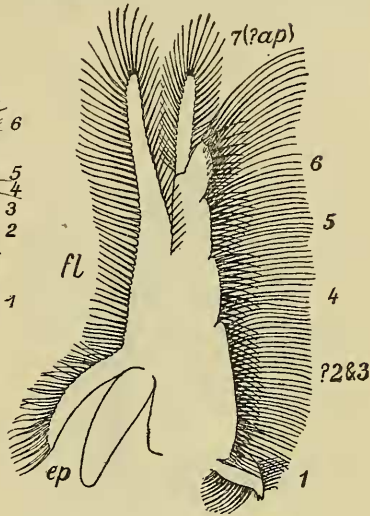
_____

* But see footnote to p. 48.

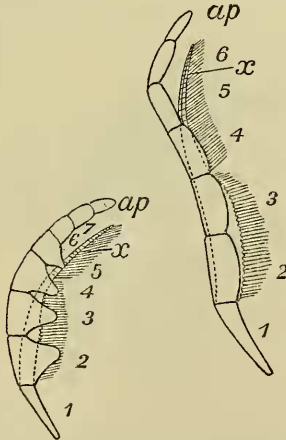Text-figure 4.

Text-figure 5.

Thoracic limb of *Chiro-cephalus* sp.

First thoracic limb of *Limnadia lenticularis*, after Sars.

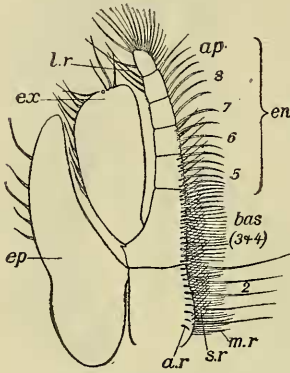For lettering see p. 71.

Text-figure 6.   Text-figure 7.

Anterior pygidial limb of *Triarthrus becki*, drawn from a model by Beecher.

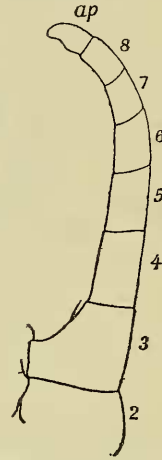One of the anterior thoracic limbs of the same.

For lettering see p. 71.

processes represents the exopodite. Probably the primitive crustacean appendage (text-fig. 2) resembled that of the Branchiopoda in being uniramous. On its outer side this limb must have

Text-figure 8.

Text-figure 9.

Thoracic limb of *Nebalia* sp.
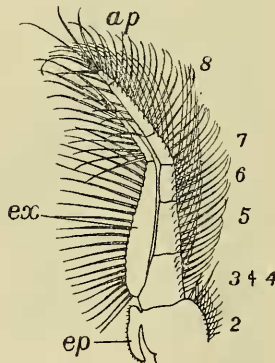
Outline of axis of thoracic limb of old female of the same.

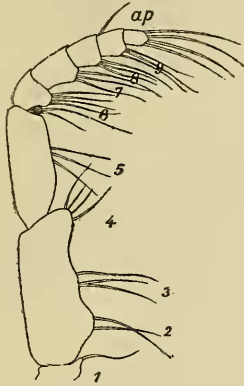For lettering see p. 71.

Text-figure 10.

Thoracic limb of *Paranebalia longipes*, after Sars, joints added after Thiele.

For lettering see p. 71.

borne near its base several epipodites. There is no necessity to suppose that these were present to the full number of the gills

and other epipoditic structures that may be found on a single
segment in various Malacostraca*. It is highly probable that

Text-figure 11.   Text-figure 12.

Maxilliped of *Calanus* sp.
For lettering see p. 71.
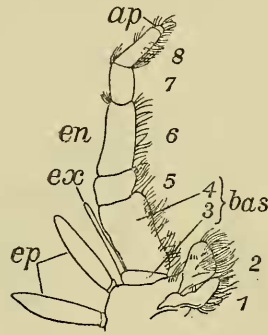
Maxilliped of *Anaspides*, after Calman.
For lettering see p. 71.

Text-figure 13.   Text-figure 14.
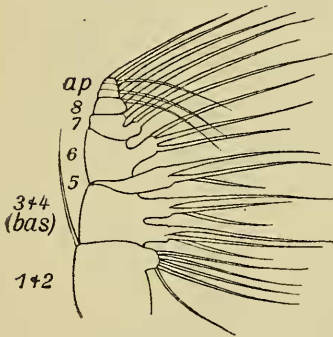
Maxilla of *Calanus* sp.
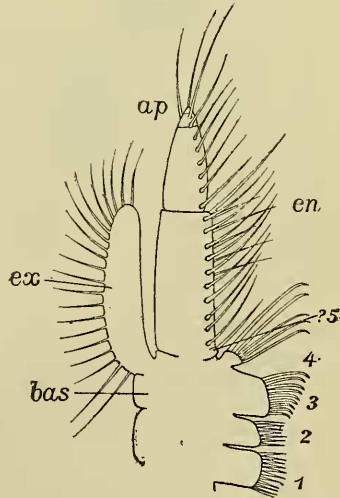
Maxilla of *Nebalia* sp.

For lettering see p. 71.

either branching and subsequent division, or meristic repetition
has taken place here. But it is not unlikely that the presence

* See Ann. Mag. Nat. Hist. ser. 7, vol. xix. p. 462 (1907).

of three epipodites (the epipodite proper and two " pro-epipo-
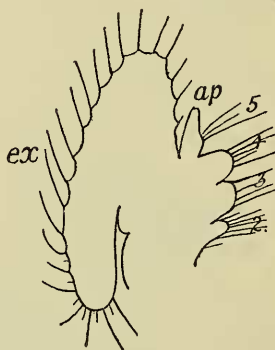dites "), as, for instance, in *Chirocephalus* (text-fig. 4), is a primitive
feature.   Beyond the epipodite stood a longer process, the
flabellum, which may have been slender, like those of Concho-
straca (text-fig. 5) and the exopodite of *Paranebalia* (text-fig. 10),
but is perhaps more likely to have been broad, like that of *Apus*
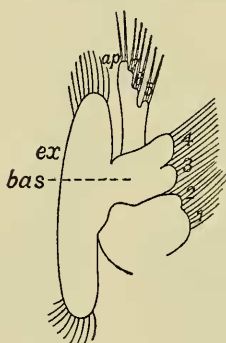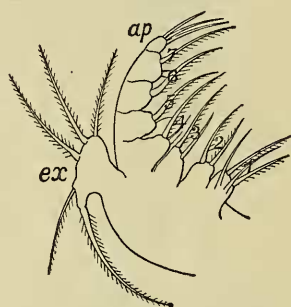
Text-fig. 15. Maxilla of *Cerataspis*, after Boas.
    „   16. Larval maxilla of *Penæus*, after Claus.
    „   17. Maxilla of *Anisocaris*, after Ortmann.
    „   18. Larval maxilla of *Palæmonetes*, after Boas.
       For lettering see p. 71.

(text-fig. 3) and the exopodites of most Leptostraca (text-fig. 8)
and of the decapod maxilla (text-figs. 15–18, and 47).   It pro-
bably extended both distally and proximally from its attachment,
like the conchostracan and notostracan flabella and the maxillary
expodite of Decapoda.   The axis of the limb ended in an apical
lobe, and on the inner edge stood a row of endites.   It does not

follow, from the fact that these, with the member resembling them which probably represents the apical lobe, number six in many Branchiopoda, that the primitive limb possessed only that quota. In certain cases the series is more numerous. Thus in Anostraca it has probably seven members [*], the maxillæ of certain decapod larvæ (text-figs. 16, 17) certainly possess eight, and the same limb of *Cerataspis* (text-fig. 15) bears nine. If, as seems likely, the first member is missing in the maxilla of *Calanus* (text-fig. 13), there is evidence here also that the series may consist of eight endites and an apical lobe. It may be that the ancestral crustacean possessed even more endites, but there is some reason for believing that it had eight only, since, as will be shown later, that number allows an arrangement which corresponds with the segmentation of the thoracic limb of Malacostraca, and with what was probably the primitive structure of the maxilla both in Decapoda and in Copepoda. If this view be adopted, there may be recognized in the primitive crustacean limb nine successive regions—eight represented by the endites and a ninth consisting of the apical lobe. These regions would be potential segments, since jointing would certainly take place between the endites rather than across them, as, in point of fact, it is seen to have done in *Triarthrus* (text-fig. 6), in the larval maxilla of *Penæus* (text-fig. 16), and in Notostraca (text-fig. 3). In the latter there may be found, immediately behind the attachment of each endite, a distinct articulation. In the case of the distal members of the series, the articulation extends only as far as the longitudinal sclerite by which the part of the axis that bears the subapical lobe, flabellum, and epipodite is separated from the rest. Just behind the flabellum, however, a very sharp jointing extends right across the limb, and another less marked articulation runs from the base of the epipodite to the inner margin, which it reaches just above the attachment of the blunt-ended proximal endite. Yet another articulation, starting from that just mentioned, joins the inner edge of the limb behind the base of the first of the large, pointed endites, thus cutting off a roughly triangular segment which in *Apus*, but hardly in *Lepidurus*, projects as a small lobe like an endite [†].

The proximal endite—the gnathobase—of the primitive limb may be judged from the evidence afforded by the Branchiopoda and *Triarthrus* to have differed in shape from the others, been directed towards the mid-ventral line of the body, and served for the manipulation of food. Probably it had a stout, blunt end, set with rows of strong, short bristles (text-fig. 27). The remaining endites were, most likely, subsimilar to one another.

5. It is natural to attempt to derive this limb from the parapodium of an Annelid ancestor. If the limb was uniramous, we must seek for analogies among uniramous parapodia, such, for instance, as those of the Syllidæ or the Eunicidæ. In the latter family

---

[*] See footnote to p. 48.
[†] See footnote, p. 48.

(text-fig. 1), the arrangement of the parts is strikingly suggestive of those of the phyllopod limb, the so-called "dorsal cirrus"—really the notopodium, whose small size and position upon the base of the large straight neuropodium make the parapodium uniramous—standing for the flabellum, the gill for the epipodite, and the short, broad, ventral cirrus for the gnathobase. Needless to say, no more than analogy can be claimed for this likeness. The point of origin of the Arthropoda from their worm-like ancestors is not to be settled merely by a general and hypothetical resemblance of the limbs.

Text-figure 19.
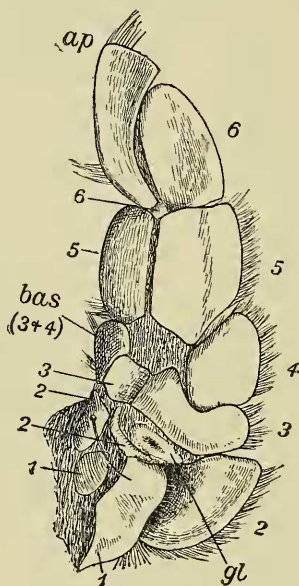
Maxilla of *Lysiosquilla maculata*.
For lettering see p. 71.

6. It has already been pointed out (p. 39) that the presence upon the hinder part of the head of Malacostraca, Ostracoda, and Copepoda of appendages not greatly modified from the assumed primitive type (text-figs. 13–21) justifies the surmise that in the original crustacean the series of similar limbs extended further forward than in Branchiopoda. Probably it resembled that of the Trilobita in including all the appendages behind the antennules, but comparison of the maxilla of the Decapoda with the pygidial limbs of *Triarthrus* suggests that there was less unlikeness between the extreme members than in that genus. Each appendage was no doubt capable of being used for swimming, for

the manipulation of food, and for respiration. In all recent Crustacea, however, the specialization of certain of the limbs for each of these functions, and for a fourth, contact with large bodies, such as prey, or the substratum, has caused them to

Text-figure 20.
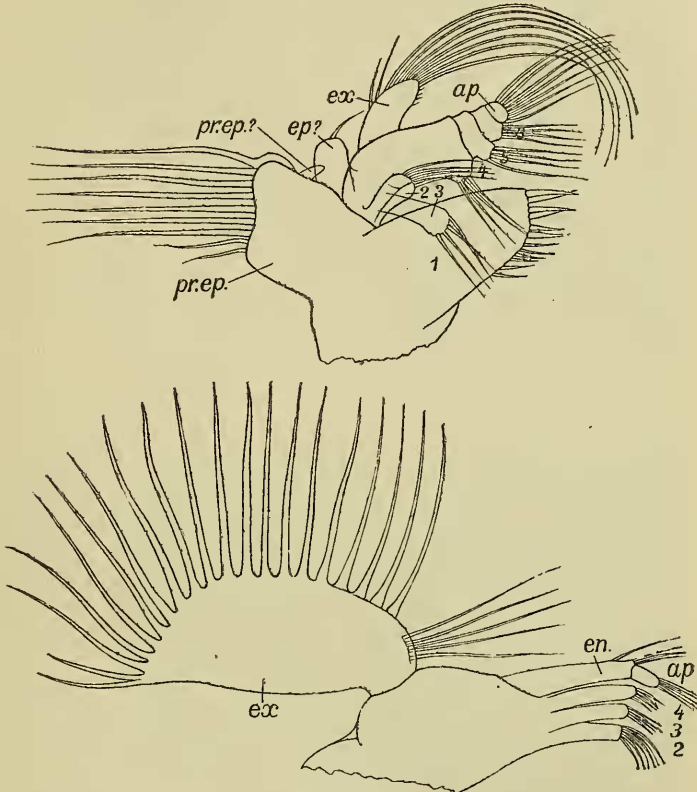
Text-figure 21.

Text-fig. 20. Maxillule of *Calanus* sp.
„   21. Maxillule of *Cypris* sp.
For lettering see p. 71.

depart in various directions from the type. Those which were specially adapted for swimming became biramous *, those for

* This change must have taken place more than once. It is already established, for instance, in the antennæ and larval mandibles of various Branchiopoda, which show no trace of it in their other limbs, and it is well developed upon the abdomen of the *Nebalia*, while it is still but incipient in the thorax. The Conchostraca (text-fig. 5), whose trunk-limbs are almost biramous, show how easily that condition can arise by an alteration in the proportions of the parts of the limb.

mastication developed the gnathobase with or without some of the
other endites, those for respiration the epipodites, and those for
contact with large objects the main axis. Generally speaking, the
limbs which in the adult are adapted to other functions than
swimming are in the larva (and were perhaps at one time through-
out life) natatory, and retain in their later condition traces of the
biramous plan, so that they may be regarded as belonging to the
biramous type. In becoming biramous, the limb has lost its leaf-
like character. This has in all cases befallen the antennæ and
mandibles, which, precociously adapted in the Nauplius to swim-
ming, never exhibit the primitive configuration. On the other
hand, the maxillæ almost invariably retain a good deal of resem-
blance to the phyllopod prototype, probably because their position
makes it impossible for them to be of much use either as jaws or
for swimming. The trunk-limbs of Branchiopoda are phyllopod,
and show in some detail the features which it is necessary to
attribute to those of the ancestral crustacean *; those of the
other groups are biramous †, with the exception of the thoracic
appendages of the Leptostraca, which exhibit various degrees of
transition from the phyllopod to the biramous condition.

---

* The lobes of the trunk-limbs of Branchiopoda (text-figs. 3–5) are exceedingly
difficult to homologate. It seems, for instance, quite possible that the Anostraca
have no flabellum, and that the structure known by that name which is jointed to
the end of their limbs corresponds to the so-called last (sixth) "endite" of *Apus* and
Limnadia. If so, however, an additional endite must be intercalated into the series
in Anostraca or excalated from it in Notostraca, for in the former group there are
six of these lobes before the terminal structure in question, but in the latter only
five. The facts of meristic variation would explain this discrepancy without
difficulty, but the actual solution is probably indicated by the presence in *Apus*,
though barely in *Lepidurus*, of what looks like a vestigial endite, standing in the
gap between the first and that which has been regarded as the second of the series.
This little lobe bears no bristles, but the section of the axis opposite it is defined by
lines of soft cuticle, such as those which mark out the segments of the other endites.
If there be here a true endite, the series in *Apus* corresponds with that of Anostraca.
Lepidurus must then be considered to have lost the second endite (though not its
segment), and in *Limnadia* it has perhaps fused with the third. It is true that
this hypothesis is open to the objection that it brings the epipodite opposite the
third endite, but such a displacement presents no great difficulty in view of the
vestigial nature of the supposed second segment, which does not reach the outer
edge of the limb, and of the fact that the epipodite is attached not wholly to the
third segment, but astride of the articulation between it and the portion of the limb
proximal to it. Again, the little process known as the "subapical lobe," present in
Apus and *Branchipus*, but barely or not at all represented in some other genera, as
Chirocephalus and *Limnadia*, may or may not represent the true end of the axis
of the limb. If it does not, then the apex must be the so-called last endite. This
(if the above conjecture with regard to the flabellum of Anostraca be true) is always
an organ *sui generis*, separated by a more or less distinct joint from the rest of the
limb. In either case, the condition of the apical lobe in the Branchipoda is
abnormal as compared with that which it shows in the larval maxilla of the
Decapoda and in *Triarthrus*, which in this respect probably more nearly represent
the ancestral Crustacea. To judge from the thoracic limbs of *Nebalia* (text-fig. 9),
whose end-joint differs strongly from the rest and is much more sharply articulated,
the appendages upon the trunk of the phyllopod ancestor of the Malacostraca must
have resembled those of the Branchiopoda in respect to the apical lobe.

† The limbs of the Trilobita (text-figs. 6, 7) present an interesting problem in
that, while they are undoubtedly biramous in the sense of consisting of two subequal
rami upon a common stem, their "exopodites" are inserted in a different position
from those of recent Crustacea or from the flabella of the Branchiopoda. The
"endopodite" of the pygidial limb (in *Triarthrus*) is clearly comparable with the

7. The relation of the parts of the biramous limb to those of its leaf-like forerunner may be elucidated by a study of actual phyllopod appendages. It would seem that the flabellum is represented by the exopodite, and the main axis, ending in the apical lobe, by the protopodite and endopodite. In regard to the exopodite, the evidence of the Leptostraca, in which it is flattened and bears just the same relation to the other parts of the limb as the flabellum, is too strong to be set aside without more convincing reasons than have been adduced. Theories which disregard this consideration depend upon the precarious support afforded by a comparison of the arrangement in various cases of the endites. These structures, however, are very variable and difficult to homologize, and in particular those of the maxilla, which in adult reptant Decapoda appear to suggest that the fifth and sixth endites have become endopodite and exopodite, have in more primitive members of the same group a quite different aspect, which supports strongly the theory stated above. The larvæ of various Carides, as, for instance, that of *Palæmonetes* (text-fig. 18), show at the base of the endopodite of the maxilla, in the region of the ischipodite, a distinct fifth endite. In other cases, as in *Anisocaris* (text-fig. 17) and *Penæus* (text-fig. 16),

---

axis of the phyllopod limb, and in shape more nearly resembles the larval maxilla of a Decapod than the trunk-limb of a Branchiopod. It is remarkable only for the comparatively unimportant facts that the region of the third and fourth endites, instead of forming a single joint (the basipodite), is divided by an articulation into two, each of which bears one endite, and that beyond the fourth endite the limb has but four segments, instead of the five which the maxilla of *Cerataspis* (text-fig. 15) indicates as the full complement of the corresponding region of the decapod limb. It does not seem impossible that an additional segment may eventually be discovered at the end of this appendage. The conditions are none too clear in Beecher's model. The "exopodite," however, stands upon the segment of the second endite, not upon that of the third and fourth. Probably this indicates that the structure here called the exopodite is not homologous with that to which the same name is applied in recent Crustacea, but is a modified epipodite. In that connection it is interesting to note that Beecher attributes to it a respiratory function. If the foregoing theory be correct, the thoracic limbs of Trilobita present a very remarkable analogy to those of Decapoda, consisting as they do of a sub-cylindrical, seven-jointed axis with a complex respiratory structure borne on the outside near the base. Unlike the podobranchs of the Decapoda, however, the epipodite of the Trilobita " contrives a double debt to pay " as gill and "exopodite.'

The foregoing interpretation of the limb of *Triarthrus* receives very interesting support from the arrangement of the parts of the mesosomatic appendages of *Limulus*. Here the axis bears on its outer side three broad exites, separated from it and from one another by sutures to which correspond notches on the edge of the limb. (The first exite of the gill-bearing limbs is, upon its anterior face, divided into about a dozen strips by less-marked sutures, of which only two remain in the genital operculum.) That part of the axis which bears the first and second exites is unjointed, but the third is attached to a well-marked segment, and beyond this two free joints form the apex of the limb. The first and second exites are crossed obliquely upon their hinder face by the gill-lamellæ. It is pretty clear that they are epipodites, and a comparison at once suggests itself between them and the very differently shaped "exopodite" which bears gill-lamellæ in *Triarthrus*. The third exite in *Limulus*, sharply distinct from the second, is no doubt the exopodite.

The supposed biramous mouth-parts of Insecta are not so in reality, and I take this opportunity of retracting the view I have expressed on that point in my ' Manual of Zoology ' (London, 1912). The lacinia and galea are, I now believe, the third and fourth endites, and the palp is the endopodite.

this is succeeded by a sixth and a seventh, while in *Cerataspis*
(text-fig. 15) the endopodite bears four endites, making eight
altogether, besides the apical lobe in the position of the dactylo-
podite. In the last two cases it is clear that the endopodite
represents the whole distal part of the limb, and not, as has been
supposed, the fifth or sixth endite only.

For a detailed comparison of the jointed stem formed by the
protopodite and endopodite of the biramous limb with the endite-
bearing axis of the phyllopod appendage, it is necessary to find
some fixed point of correspondence between members of the two
series. It would be natural to look for this at the base of the limb,
but the development of *Penæus* and other Decapoda, during which
the basal joint of the appendages of the thorax recedes into the
side of the body, is a warning against the use of such a method.
On the other hand, the differences in the total number of endites
in different limbs makes it useless to start a comparison from the
distal end. The epipodites vary in number, and their homologies
are doubtful, so that their points of attachment afford no reliable
clue. There remains the flabellum-exopodite. It is unfortunate
that the uncertainty which exists in regard to the homologies of
the endites of Branchiopoda makes even the seat of the flabellum
a doubtful point in that group, but, as will be seen, what can
be stated on this point is not without its uses in confirming the
evidence of other classes. In the Anostraca (text-fig. 4) the
flabellum is probably absent. In Conchostraca (text-fig. 5) it
stands opposite the junction of the second and third endites of a
series of six, but, quite possibly, these two members represent the
third and fourth of the full series, the second, which is present
in the Anostraca, being in Notostraca vestigial and in Concho-
straca either lost or fused with the third to form a single
elongate lobe. In Notostraca (text-fig. 3), where the whole axis
of the limb is more or less strongly segmented, the flabellum
stands on the segment of what may be the third or the fourth
endite. In the maxilla of the Malacostraca (text-figs. 14–18, and
47) the situation is clear. Here the exopodite arises opposite the
third and fourth endites, upon a region of the limb which may be
undelimited, as in most Decapoda, but which is often marked off
more or less completely to form a segment, as in Leptostraca
(text-fig. 14), Mysidacea, Cumacea, Euphausiacea, and the decapod
larva *Anisocaris* (text-fig. 17). Where there is no exopodite,
as in Isopoda, Amphipoda, and Stomatopoda [*] (text-fig. 19), a
segment with two endites is found in the same position on the
maxilla as on that of the orders in which the limb bears an
exopodite. The maxilla of *Calanus* (text-fig. 13) agrees remark-
ably in structure with that of Malacostraca. Though it has no

---

[*] In the maxilla of the Stomatopoda, the basipodite is represented upon the
outer side of the limb by a single sclerite, but the segment of the third endite is
differentiated from that of the fourth by the possession of a sclerite of its own upon
its hinder face. The structure of this rather puzzling limb is elucidated in text-
fig. 19. It is interesting to note that the maxillary gland opens on the second
joint, like the antennary gland of Mysidacea and Amphipoda.

exopodite, there may be found in its proximal half a double segment bearing two endites. At first sight, the endites upon this segment appear to be the second and third, but the length of the segment which precedes it, and the position of the endite upon the latter at its distal end, suggest at once that that is also a double segment, that here, as in Carides, the first endite has been lost, and that the second double segment therefore bears the third and fourth endites and is the basipodite. This impression is strengthened by the fact that beyond the segment with two endites there are five simple segments, as there are beyond the endites which represent the basipodite of *Cerataspis* (text-fig. 15), which, since in that respect it agrees with the thoracic limbs of Malacostraca, may be taken as indicating the original number of segments in this region in the malacostracan maxilla. In the maxillule of *Calanus* (text-fig. 20) the first endite is carried upon a fairly distinct segment, but the second, third, and fourth lie upon a region which is undivided save by an incomplete constriction, which marks off the distal portion of

Text-figure 22.   Text-figure 23.

Maxillule of *Lepas* sp.   Mandible of *Lepidurus* sp.

it, where the fourth endite and the exopodite are borne. The maxilliped of *Calanus* (text-fig. 11) has a very short basal segment bearing the small first endite, a long second segment bearing the second, third, and fourth endites, and six distal segments, which is one more than might be expected. Meristic rearrangement has probably been at work in this portion of the limb*. The maxillule of *Cypris* (text-fig. 21), which curiously simulates the maxilla of Carides, seems, like the latter appendage, to have lost the first endite. If that be the case, the exopodite here stands opposite the third and fourth endites. The thoracic limbs of *Nebalia* (text-figs. 8, 9), though they present no endites,

* An increase beyond the normal of the number of joints in a crustacean limb may take place in three ways : (1) by the annulation of the unsegmented apex of either branch of the limb to form a "flagellum," as in antennæ, thoracic exopodites, and pleopods of Malacostraca, etc. Three faint annulations upon the apical segment of the maxilla of *Calanus* are probably of this nature; (2) by subdivision of a segment, as in the carpopodite of various Carides; (3) by resegmentation of a limb or of part of it, as probably in the maxilliped of *Calanus*.

4*

are instructive in regard to the segmentation of the phyllopod limb. Here the number of the segments which are formed in the endopodite varies with the limb and with the age and sex of the individual. Nearly always the four distal segments can be made out, and often a fifth is to be found proximal to them, leaving a long basipodite, which is always clearly marked off from the coxopodite. Across the basipodite, distal to the exopodite, there

Text-figure 24.
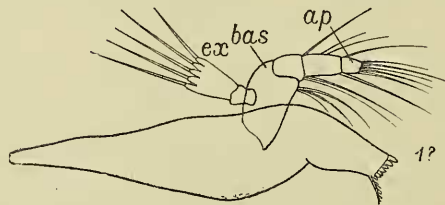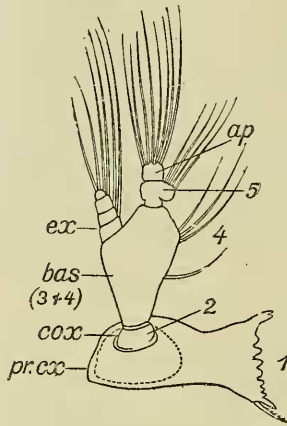
Text-figure 25.

Text-fig. 24. Mandible of *Calanus* sp.
„   25. Mandible of *Cypris* sp.
For lettering see p. 71.

occasionally appears an additional joint, the faintest of the series, indicating the double nature of the segment *.

* It is perfectly true that most of these segments are without muscles, but from that it does not follow that their evidence may be disregarded. Probably they are vestigial, having lost their endites, and not, as where the limb becomes subcylindrical, acquired a value of their own. The division of the basipodite probably occurs also in *Anaspides* (text-fig. 12), where, in the anterior thoracic limbs, the endopodite appears to contain six joints, but is flexed between the third and fourth of these, not between the second and third as in the Eucarida. It seems likely that the first

It appears, then, that the flabellum-expodite, which in the unjointed limb arises opposite the third and fourth endites, is, when the appendage becomes jointed, generally borne by a double segment, representing those of both the lobes in question, but if, as occasionally happens, the two components of this segment become distinct, the exopodite may be found either upon the proximal of them (*Nebalia* etc.) or upon the distal (maxillule of *Calanus*, Notostraca?). Thus in the axis of the phyllopod limb the region of the third and fourth endites corresponds to the basipodite of the biramous limb, that of the first two endites to the rest of the protopodite, and all that part which lies beyond the fourth endite to the endopodite. The doubleness of the basipodite makes necessary certain terms for the distinction of its parts. Its two components may be known as the *probasipodite* and *metabasipodite*, and when either of these alone acts as the basipodite by bearing the exopodite, it is a *hemibasipodite*. In contradistinction to this the complete double joint may be called the *symbasipodite*.
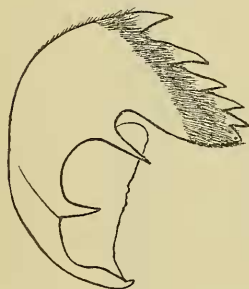
Text-figure 26.   Text-figure 27.

Mandible of *Lepas* sp.
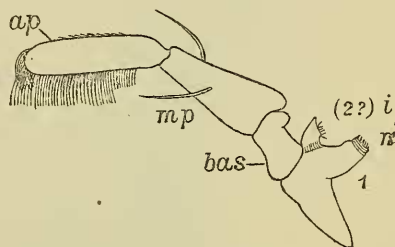
Mandible of *Nebalia* sp.
For lettering see p. 71.

In the proximal part of the branchiopod limb, the most persistent of the epipodites stands opposite the second endite. The segment to which these structures belong is the coxopodite. If other epipodites (pro-epipodites) be present, they stand in the region of the gnathobase. This region is the so-called "precoxa," or "pleuropodite," which may or may not have originally existed as a free joint in every biramous limb, but has now nearly always

---

segment after that which bears the exopodite is here not the ischiopodite, but the second division of the basipodite, or, as it may be called, the *metabasipodite*. If this be so, the question arises whether the basipodite be not divided in the Pericarida, whose thoracic endopodites also are flexed between the apparent third and fourth joints. But in that case their apical joint must represent the fused propodite and dactylopodite. With Calman, I am unable to regard the so-called "stylopodite" as more than an enlarged, terminal spine. If it be one of the primary members of the axis of the limb, it must represent the apical lobe, and the total number of joints in the axis becomes ten, as in the maxilliped of *Calanus*.

disappeared, either by fusion with the trunk or with the second
joint, or perhaps sometimes by excalation.

The fifth endite and those distal to it belong to that part of the
limb which stands beyond the attachment of the flabellum, and
represent the endopodite of the biramous limb. The maxillæ of
Cerataspis and larval Natantia (text-figs. 15–18) seem to show
that each of these endites is borne upon a portion of the limb
which represents a single joint of the biramous appendage, and
that the apical lobe is an unsegmented distal region of varying
extent, corresponding to the dactylopodite and any adjacent
segment or segments not represented by an endite.

Text-figure 28.
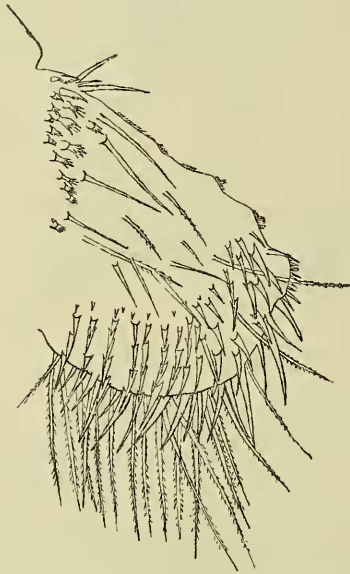
Gnathobase of thoracic limb of *Lepidurus* sp.

It is fair to assume that all these relations existed in the
primitive crustacean appendage, and that the latter gave rise to
the biramous limbs by a transformation in which the axis of the
limb became jointed in the way indicated, the endites in great part
or altogether disappeared, and the flabellum approximated in shape
to the distal part of the axis and came to stand side by side with
it at the end of the third (or, if the precoxa were not separate,
the second) joint of the limb.

8. With the original phyllopod limb, thus reconstructed, the
jaws of Malacostraca may be compared as follows:—In the

mandible, homologues must be found for the molar process, the incisor process, and the palp. The molar process pretty clearly represents the mandible of the Branchiopoda, and through that the gnathobase of the phyllopod limb. The grinding-surface of the mandible of *Chirocephalus* (text-fig. 30) is covered by two comma-shaped patches of fine ridges, each ridge consisting of a row of tubercles, which perhaps represent the rows of stout bristles upon the end of the gnathobases of the trunk-limbs of Notostraca (text-fig. 28). In places the ridges bear some hairs. The commas are reversed, so as to fit against one another, and one patch is narrower then the other and composed of coarser ridges. In view of its structure, position, and function, there can be little doubt that this organ is a specialized gnathobase.

Text-figure 29.   Text-figure 30.
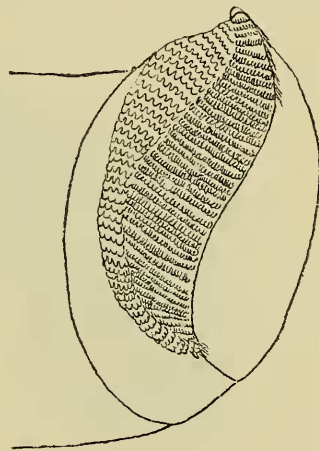
End view of maxillule of *Lepas* sp.   End view of mandible of *Chirocephalus* sp.

Two sets of ridges, very similar to those on the mandible of *Chirocephalus*, may be recognized at the end of the molar process in *Nebalia* (text-fig. 31), though here one is of less extent than the other, and seems largely to have been replaced by rows of delicate hairs. Fine ridges, as may be seen in the figures given by various authors, exist also upon the molar processes of various Malacostraca (*Anaspides*, *Gammarus*, etc.). In the Decapoda a crescentic or comma-shaped set of serrated ridges is often present (text-figs. 32, 43), with or without patches of hairs and granules, though they tend to disappear, and the molar surface is often broken up into a small number of large lobes. The ridges vary greatly in width, degree of salience, and serration, but are often

much like those of *Nebalia* (text-figs. 38–43). Clearly, we have
here the mandible of *Chirocephalus* in process of further evolution.
The homology of the incisor process is more puzzling. No trace
of it can be found in the Entomostraca. In *Lepidurus* (text-
fig. 33) the end of the mandible, instead of being oval as in
Chirocephalus, is elongate, tapering to one end, and slightly
curved. It is crossed by deep ridges, few in number, and marked
each by a few coarse tubercles. The narrow end stands away
from the rest, bears three or four teeth instead of the ridges on
the wider part, and somewhat suggests an incipient incisor
process, but this is at the hinder end of the organ, whereas the
incisor process of Malacostraca is anterior. It seems likely that

Text-figure 31.
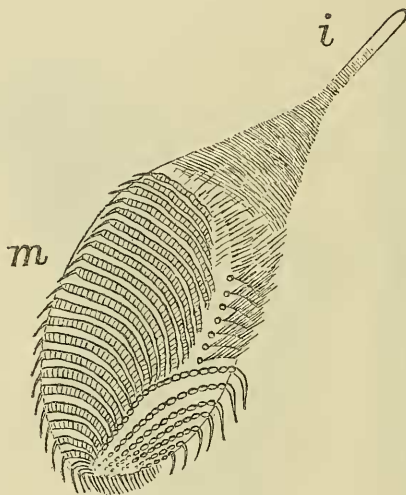
End view of mandible of *Nebalia* sp.

For lettering see p. 71.

the biting-surface of the mandible of Notostraca represents one
of the two sets of ridges found in the same position in *Chiro-
cephalus*. In *Calanus* (text-fig. 35) the condition is not dissimilar.
The biting surface is narrow, elongate, tapering towards the
ends, especially towards the hinder end, and crossed by coarse
ridges, variously tuberculate. At the anterior end stands a
structure which at first sight a little recalls the incisor process,
but in an end view of the mandible this is seen to be only the
first ridge, removed a little from the rest and connected with
them by a flange. The mandible of *Cypris* (text-fig. 34) is of
the same type, but the anterior ridge is less outstanding and not

flanged to the next, the ridges are more regular, the valleys between them bear spines, and at the hinder end there is not, as in *Calanus*, a single long, fringed spine, but a pair. Probably the biting-surfaces of the mandibles of *Calanus* and *Cypris* are homologous with one another and with that of *Lepidurus*. The mandible of *Lepas* (text-figs. 26, 36) is a very different structure, thin, with a sharp, toothed edge, and in side view very similar to the incisor processes of certain Decapoda. It is crossed near the base by an articulation, and it seems possible that its toothed edge represents, not the gnathobase, but the second endite. On the other hand, the maxillule of the barnacle (text-figs. 22, 29), which appears to be built on the same plan, is of a fair width at the end, and crossed by short ridges, each bearing a row of five spines, so that this limb forms a sort of transition from the ridged condition of *Cypris* to that of *Lepas*. Unless the mandible of the barnacles be homologous with the incisor process, the latter
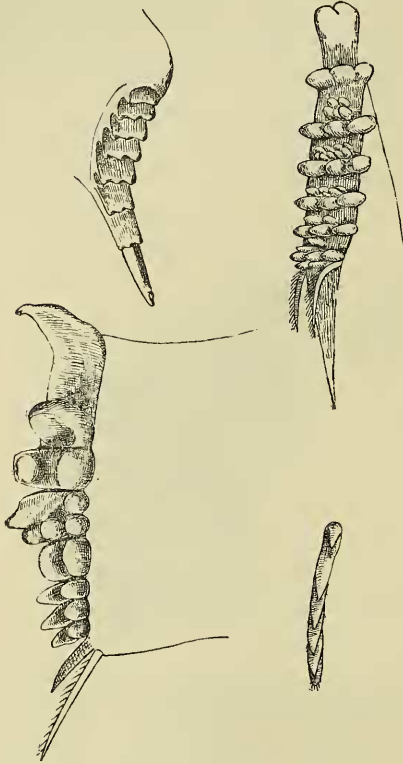
Text-figure 32.
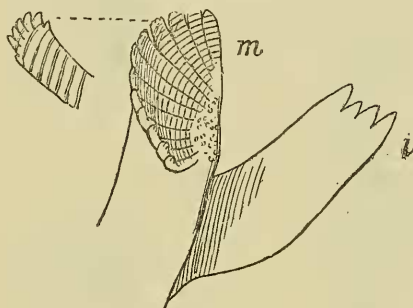
End view of mandible of *Desmocaris*.

For lettering see p. 71.

is a structure peculiar to the Malacostraca, and not to be found even in rudiment upon the mandible of any other crustacean. Two modes of origin can be suggested for it. It may be regarded either as an outgrowth from the gnathobase or as representing the second endite. On the whole, the latter is the more plausible view. From its first appearance in *Nebalia* (text-figs. 27, 31) this process has a knife-edge, quite unlike the ridged surface of the molar process and its homologues, although it often comes to bear a row of teeth. As has been shown, there is no trace in phylogeny of its origin from the proximal part of the limb, and, though in ontogeny (as, for instance, in that of *Penœus* or the Stomatopoda) it and the molar process may originate from the same simple precursor, this is no more than the differentiation, in the course of development, of the rudiment of the appendage, and happens also in the case of the palp. If this view be correct,

the basal joint of the mandible of Malacostraca corresponds to
the fused precoxa and coxopodite.   Those of Branchiopoda
represent the precoxa only, the rest of the limb having dis-
appeared.   The basal segment of Copepoda, again, corresponds
to no more than the precoxa, the coxopodite being represented

Text-figure 33.   Text-figure 34.

Text-figure 35.   Text-figure 36.

Text-fig. 33. End view of mandible of *Lepidurus* sp.
    ,,   34. End view of mandible of *Cypris* sp.
    ,,   35. End view of mandible of *Calanus* sp.
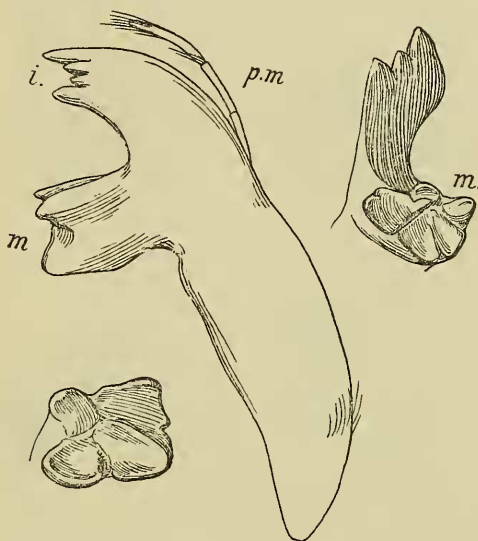   ,,   36. End view of mandible of *Lepas* sp.

by the little segment between that which bears the biting-edge
and that upon which stand the exopodite and endopodite in
Calanus (text-fig. 24).   In Ostracoda (text-fig. 25), it would seem,
the coxopodite must either have been excalated altogether or

have fused with one of the adjoining segments.   The mandibular palp represents the remainder of the axis of the limb.   Its first segment is undoubtedly the basipodite, though there is nothing to show whether it is a complete symbasipodite.   Often a joint divides the remainder into two parts, but these cannot be regarded as corresponding with any of the normal segments of the endopodite [*].

The mandible of the Crustacea is an exceedingly complicated, varied, and interesting organ, presenting many problems and worthy of a great deal more attention than it has received.

Text-figure 37.   Text-figure 39.

Text-figure 38.

Text-fig. 37. Left mandible of *Leander serratus*.
   „   38. End view of molar process of the same limb.
   „   39. End view of right mandible of *Leander serratus*.
For lettering see p. 71.

The laciniæ of the malacostracan maxillule (text-fig. 46) represent the first and third endites.   This is suggested, though hardly proved, by the condition of the limb in *Nebalia*.   Hansen has shown that in various other genera the laciniæ belong to the first

[*] G. W. Smith (Q. J. M. S. liii., iii. p. 506, 1909) describes a mandibular palp in *Paranaspides* which would be quite unique among such structures in the Malacostraca, having four joints and an exopodite. I am unable to confirm this. All the specimens in the British Museum have three joints and no trace of exopodite.

and third segments. In many Decapoda, as in *Leander* (text-fig. 46) the same fact is clear upon careful examination. I shall call the processes in question the *inner and outer laciniæ*. The outwardly-directed lobe which is often present upon the first segment has been regarded by various authors as the exopodite, and the conclusion drawn that the part of the limb proximal to the basipodite is lacking. It is hard to see upon what evidence this view can be based. The exite is much more easily interpreted as a proepipodite. It is represented in *Leander* by a hump upon the base of the first endite.
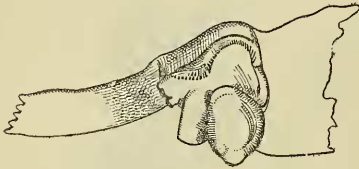
Text-figure 40.   Text-figure 41.
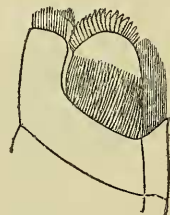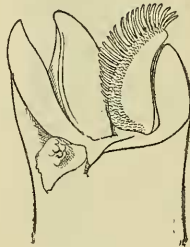
Text-figure 42.   Text-figure 43.

Text-fig. 40. End view of left mandible of *Conchodytes tridacnæ*.
　　　 ,,　　41. End view of left molar process of *Periclimenes spiniferus*.
　　　 ,,　　42. Oblique view of end of right molar process of the same species.
　　　 ,,　　43. Same view of right molar process of *Saron marmoratus*.

The two cleft lobes usually known as the "laciniæ" of the maxilla (text-figs. 14–17) are each equivalent not, as has sometimes been supposed, to one of the elementary segments of the limb, but to two, and thus they together represent the first four endites of the primitive limb. This interpretation is strongly suggested by such appendages as the maxillæ of larval Penæides (text-fig. 16) and especially by that of *Cerataspis* (text-fig. 15), and is not contradicted by the fact that articulations are often

not developed between the first and second or between the third and fourth segments—as, for instance, in *Anisocaris* (text-fig. 17), which is an instructive case of this condition. The first endite is frequently absent, whether or not its segment be present as a separate entity. In the Peracarida, the number of endites is generally reduced in this way to three (or fewer, if another of them be absent), though the Mysidacea at first appear to form an exception. In *Mysis*, however, closer examination reveals a condition which may be described as follows. The edge of the second segment proximal to its endite is rounded, meets the base of the endite in a notch, and bears a row of bristles which is continued from the notch across the origin of the endite. The notch forms an outline which simulates the cleft lobe formed in Eucarida by the first two endites. If this suggestion be correct, the Mysidacea, liike other Peracarida, must be regarded as having lost the first endite of the maxilla. In Leptostraca (text-fig. 14), Anaspidacea, Stomatopoda (text-fig. 19), and typical members of the Eucarida (text-figs. 15–17), it is present. The degree to which the first and second, and again the second and third, endites are associated to form cleft lobes varies, and is highest in some Decapoda. I shall allude to these double structures—the so-called " laciniæ " of the maxilla—as the *first and second lobes*. The first comprises the endites of the precoxa and coxopodite, the second those of the basipodite. The fifth endite is often represented in the adult by a slight swelling at the base of the endopodite. The exopodite (scaphognathite) is a little-modified flabellum, and a small rounded lobe proximal to it in Eucarida perhaps represents the epipodite.

In the first maxilliped of Decapoda (text-fig. 48) the third and second endites are distinct. The latter is often marked by a slight notch, which, however, is not likely to indicate the presence of the first endite, the precoxa being probably fused with the body in the thoracic segments of this group. In *Anaspides*, as is shown by the history of the development of the gill-rudiments (text-fig. 12), the first and second endites are both present, and the basal joint carries also two epipodites, from which it would appear that the precoxa in this genus is fused with the coxopodite. The Peracarida probably agree with *Anaspides* in this respect, as they have two epipodites (oostegite and gill) upon the basal joints of the thoracic limbs. Endites may be present upon the endopodite of the maxilliped in the Peracarida, as in *Mysis* (and perhaps also in *Gammarus*, but in the latter there is some doubt about the identity of the apparent ischiopodite which bears the endite in question : see footnote to p. 53). Knobs bearing bristles which sometimes appear upon the coxopodites of the second and third maxilliped of prawns (text-figs. 49, 50) may represent the second endite, and a similar knob in the sternal region at the base of the second maxilliped may be a vestige of the gnathobase.

III.

1. The mandible of the Palæmonidæ (text-fig. 37) is deeply cleft into two diverging processes, both directed obliquely towards the median plane of the body. One of these—the incisor process —is a thin structure, more or less ribbon-like in the Pontoniinæ and *Desmocaris* (text-figs. 32, 40), but shorter and broader in *Leander serratus* (text-fig. 37). It trends, at its base, downwards, but curves inwards and at the same time twists its outer edge forwards, so that, while at its base it is nearly vertical, with its width transverse to the body, at its free end it is nearly horizontal, with its width longitudinal to the body. The other—the molar process —is stout and subrectangular in section, and slants dorsally, to end somewhat obliquely truncated on the median plane. In the Palæmoninæ a delicate palp, usually three-jointed, stands on the anterior side of the limb, at the base of and just dorsal to the incisor process, along whose outer edge it curves towards the middle line of the body. The only Pontoniinæ which possess a mandibular palp are *Urocaridella* and *Palæmonella*. In these it is two-jointed.

The incisor process of Pontoniinæ usually ends in three teeth, the midmost of which is shorter than the others, but there are sometimes more. Thus in *Coralliocaris japonica* there are four on one mandible and five on the other, and in *Conchodytes tridacnæ* (text-fig. 40) there are on one side five, nearly equal, and on the other six. In *Leander serratus* (text-fig. 45) there are two large teeth, with on the right mandible one, and on the left two, smaller intermediate teeth. In *Desmocaris* (text-fig. 32) there are four teeth on the right and five on the left mandible, those at the outer ends of the row being rather larger than the others. In each case the arrangement is not such that the teeth of the two sides can closely interlock. The molar process of most Palæmonidæ (text-figs. 38–42) ends in a roughly square concave surface, around which is an incomplete wall composed of from four to six projecting lobes. Some of these have crescentic or horseshoe-shaped rims, with their open sides towards the middle of the process. Others are completely rimmed, but raised more on the outer side than on the inner. In *Leander serratus* (text-figs. 38, 39) there are four sharply distinct lobes. The lobes differ a good deal in shape, and there is only a general correspondence between those of the mandibles of the two sides. So far as this correspondence goes, it is not the mirror-likeness usually found in paired structures, but the two arrangements are reversed, so that there is a rough sort of interlocking. In *L. serratus* the lobes are only roughened in places. In the Pontoniinæ one lobe, and part of the rest of the surface, bears a fur of bristles or is roughened by tubercles. This, I believe, is the last remains of the clothing of bristles found on the end of the molar processes of other Carides, such as the Alpheidæ. In the primitive Palæmonid *Desmocaris* (text-fig. 32) the process

ends in a semicircular surface, which bears a comma-shaped patch of serrated ridges. Sollaud, who called attention to the difference between the molar surfaces of *Desmocaris* and those of other Palæmonidæ [*], pointed out that these ridges also occur in the Acanthephyridæ, and regarded them as a primitive feature. In this he is probably right, since, as I have shown, a similar arrangement is found in *Nebalia* and certain Branchiopoda. In *Amphibetæus* and some Hippolytidæ (text-fig. 43) part of the surface is covered with such ridges and part with bristles, and lobes of various shapes are appearing. We have here probably a transition from the ridged condition to that which is found, for instance, in Pontoniinæ.

Text-figure 44.
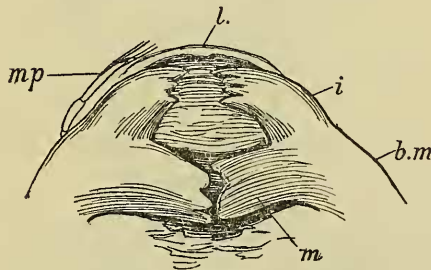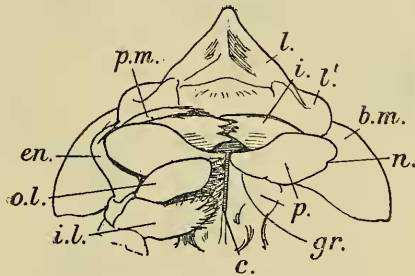
Text-figure 45.

Text-fig. 44.—Ventral view of mouth-parts of *Leander serratus* after removal of maxillipeds, maxillæ, and left maxillule.

Text-fig. 45.—The same after removal of maxillules and paragnatha.
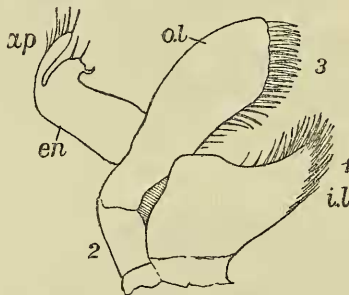
For lettering see p. 71.

2. The mandibles lie (text-figs. 44, 45) in a chamber enclosed between the lips, the hood-like labrum standing in front of them, and the large bilobed metastoma behind, while the swollen bases of the mandibles themselves close in the chamber at the sides.

[*] C. R. Ac. Sci. clii. p. 913. (1911).

There are two openings to the lip-chamber—a narrow median slit between the lobes (paragnatha) of the metastoma and a wider transverse gap between the metastoma and the labrum. The incisor processes close the transverse opening, meeting in the middle line. The molar processes meet deeper in the chamber, just under the opening of the gullet.

3. In the maxillule (text-fig. 46), the inner lacinia, which is usually the narrower of the two, curves towards the outer and is provided with relatively feeble bristles. The outer lacinia has very stout, yellow bristles and is probably the only structure, other than the mandible, which is capable of tearing the food. The endopodite is bifid at the tip, the proximal branch, which possibly represents an endite, being curved in a short spiral, the distal branch nearly straight. The maxillules stand close against the paragnatha (text-fig. 44), the laciniæ of each opposed to those of the other across the median line, but not quite meeting them.
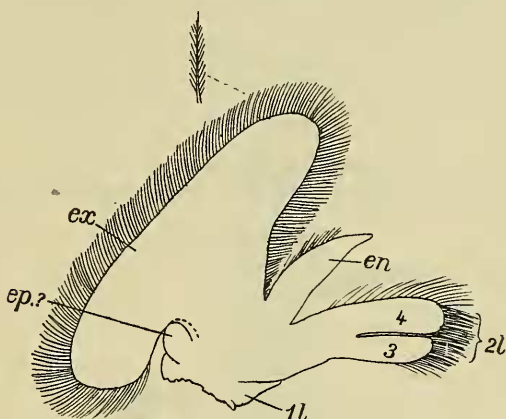
Text-figure 46.

Maxillule of *Leander serratus*.

For lettering see p. 71.

The inner laciniæ are just behind the cleft of the metastoma, the outer stand beside the cleft. The endopodite is directed outwards and hooks its curved process around the outer edge of the paragnathum, which has a notch to receive it. Probably this gives a purchase for the action of the limb.

4. In the maxilla (text-fig. 47), the first double lobe has disappeared and is represented only by a slight swelling of the edge of the limb. The second lobe is of good length, but tends to become simple in the Pontoniinæ. In this respect it is very variable, the maxillæ of the two sides sometimes differing in an individual. From the frequent occurrence of reduction in the lobes of this limb in the Carides, it would seem that they are structures of no great physiological importance. The endopodite is of simple shape, tapering distally, and the exopodite (scaphognathite) varies in shape and width with the gill-chamber, and
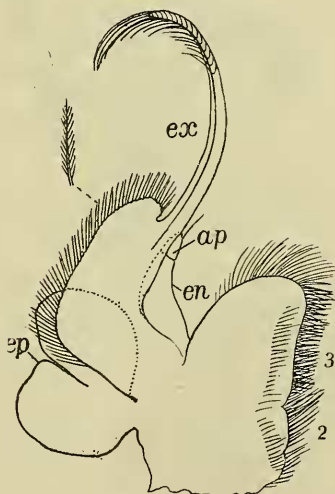
thus with the habit of body. The long bristles which fringe the
scaphognathite are feathered, which probably makes the organ
more efficient in sweeping the gill-chamber.

Text-figure 47.

Maxilla of *Leander serratus*.
For lettering see p. 71.

Text-figure 48.

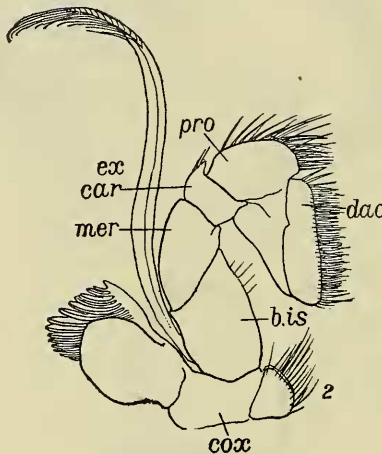

First maxilliped of *Leander serratus*.
For lettering see p. 71.

5. In the first maxilliped (text-fig. 48), two endites—the
second and third—are nearly always recognizable, and usually

separated by a very distinct notch. The notch in the proximal
endite, though less distinct, can often be made out. The endo-
podite is simple with a stout bristle near the top, and often
indications of a joint a little further down. At the tip of the
exopodite a few small joints may be present and at its base on
the outer side is a fringed lobe (lobe *a* of Boas) which varies in
width with the body and has perhaps some function in regard to
the current which the scaphognathite sets up in the gill-chamber.
Its bristles are feathered like those of the scaphognathite. The
epipodite varies much in size, and its outer border is usually
notched.

6. In the second maxilliped (text-fig. 49), the main axis
consists of six joints, the basipodite and ischiopodite being fused.

Text-figure 49.

Second maxilliped of *Leander serratus*.
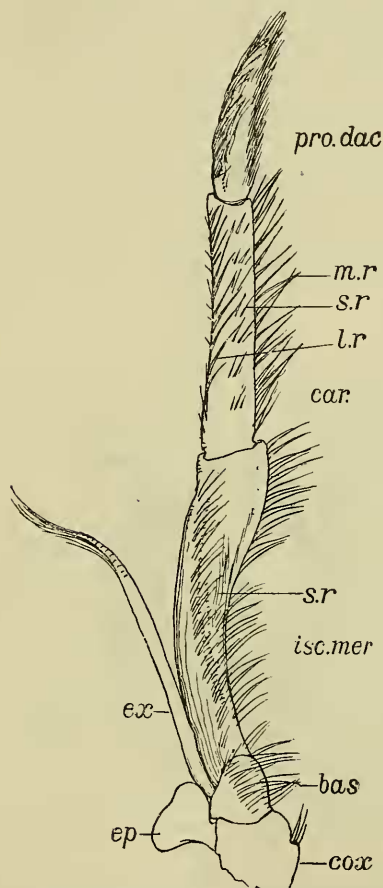For lettering see p. 71.

The last two joints are bent strongly backwards on the inner
side of the limb, so as to lie parallel with the ischiopodite, and,
owing to the backward (morphologically forward) growth of a
process of the propodite on the outer (morphologically inner) side
of the dactylopodite, the latter comes to lie along the median side
of the former, instead of at its apex. Thus these two joints are
compacted into a firm plate, which presents a long median
margin, fringed with bristles, against its fellow of the opposite
side. This is, of course, the typical caridean condition of the
limb. The exopodite is obscurely annulate in the greater part of
its length, and bears at the end a comparatively small number
of true joints. The coxopodite carries on the outer side a simple
epipodite (mastigobranch), at the base of which may be a gill
(*Leander, Urocaridella*) or the vestige of one. On the median side

of the coxopodite is a knob, which bears bristles, and may represent
an endite.   A sternal swelling which is sometimes present at the
base of the coxopodite may represent a precoxal endite.

7. The main axis of the third maxilliped (text-fig. 50) consists
of four or five joints (five in *Leander* and in *Urocaridella*, four in

Text-figure 50.
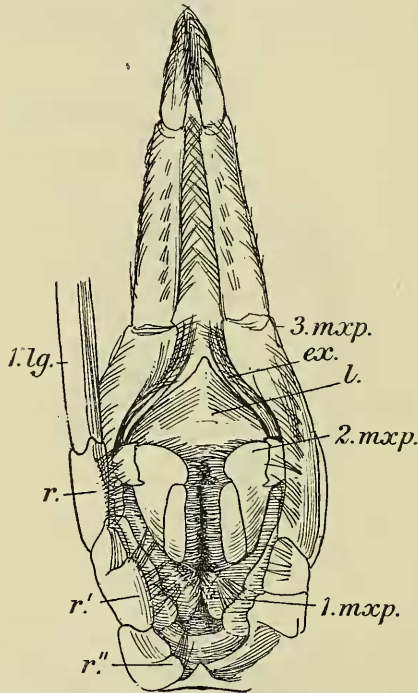

Third maxilliped of *Leander serratus*.
For lettering see p. 71.

most Pontoniinæ), the propodite being always fused with the
dactylopodite and the ischiopodite with the meropodite, and often
also the basipodite with the ischiomeropodite, in which case the
junction is generally marked by a notch.   The coxopodite bears
on the outside a small rounded epipodite, and often on the inside

5*

a bristly knob which is perhaps an endite. The exopodite is obscurely annulate, and at its end there are usually a few longer segments which are sometimes true joints, but in other cases appear to be marked merely by a change in the width of the organ and the attachment of bristles. The ischiomeropodite is almost always more or less curved, with the concave side towards the middle line of the body. It is ribbon-like and shows in the Pontoniinæ a tendency to widen. The curving of this joint brings the last two joints near to those of the fellow limb, so

Text-figure 51.

Ventral view of mouth-region of *Leander serratus*, all mouth-parts being in place.

that, while the ischiomeropodites lie at the sides of the mouth with a wide gap between them in which the second maxillipeds are exposed, the distal parts of the limbs lie side by side in front of the mouth-region. A further complexity in the arrangement of the parts of the limb is brought about by the fact that the ischiomeropodites are twisted, so that the flat surface of the appendage, which in its distal part is in a horizontal plane, is in the proximal part in a plane between the horizontal and the

vertical. This arrangement, combined with the presence of a fringe of bristles along the inner edge of the limb, has the effect of forming a kind of basket below the mouth-region, walled in at the sides by the ischiomeropodites and by the bristles which project downwards and inwards from their edges. In *Leander* * there are bristles borne in a diagonal row along the ventral surface of the ischiomeropodite, and also upon ridges of the coxopodite, basipodite, and ischiopodite of the first leg (text-fig. 51), which complete the basket behind and below, but these are less well developed or absent in Pontoniinæ. In front of the mouth, the distal parts of the third maxillipeds, with their bristles, afford a surface, horizontally placed below the antennal region while the appendages are outstretched, which by bending can be brought ventrally under the mouth so as to complete its enclosure anteriorly. The last joint often possesses along its inner side a thick brush composed of tufts of hairs more close-set than the bristles of the rest of the limb. This arrangement, which is particularly well developed in *Leander*, has probably some special function, but I have not been able to discover what that may be.

IV.

1. It is not an easy matter to induce *Leander* to feed at a given moment, and still less so to observe what it is doing while it feeds. The animal will not take food if it is not hungry, if it is languid owing to lack of aeration of the water, or if it is suffering from shock, though sometimes it will feed surprisingly soon after violent operations, such as the removal of limbs. I have tried to observe the action of its jaws by means of a mirror, but without much success. The best method is to fasten the prawn upon its back in a shallow vessel of sea water by means of plasticine. It will often feed quite freely in this position, and its jaws can easily be reached with a needle. When it is feeding, small particles of food may be seized by the chelipeds of either pair, and by them conveyed to the mouth, where they are generally received by the second maxillipeds, though sometimes they appear to be placed directly in charge of more dorsally placed structures, probably the maxillules. A large morsel occasionally appears to be steadied by the legs of the second pair, while those of the first tear off fragments and carry them to the jaws, but it is more often placed as a whole within the grasp of the second maxillipeds, which hold it in place while pieces are torn off it by deeper-lying organs, probably in the main by the incisor processes. In handling bulky masses of food, the chelipeds are assisted by the third maxillipeds, which bend back their last two joints for this purpose. The third

---

* In this genus, in which the bristles of the third maxilliped are best developed, there may be made out three bands along the limb—an inner, middle, and outer, perhaps corresponding to the marginal, submarginal, and lateral of the four series found by Claus in *Nebalia* (text-fig. 8, p. 42). Each band consists of a succession of little transverse rows. Towards the ends of the appendage the bands converge and become merged.

maxillipeds are also capable by the same action of scooping up
food and unaided conveying it to the second maxillipeds, between
which they sometimes thrust it with their tips. During these
processes the basket which has been mentioned seems to serve
the purpose of keeping the food under control till it has been
seized by the second maxillipeds. These are very important
organs, and play an indispensable part in passing food to the
mandibles. The animal can still feed if the legs and third
maxillipeds have been removed, but if all the other organs be
left and the second maxillipeds cut away it is apparently incapable
of taking food. The second maxillipeds have three principal
movements. In one, the broad flaps in which they end open
downwards like a pair of doors, and with their stout fringes
gather up the food ; in another they rotate in the horizontal plane
to and from the middle line of the body and thus narrow or
widen the gap between them ; in the third the bent distal part of
the limbs tends to straighten so as to brush forward any object
which lies between them. Frequently these movements are
combined. Once the food is past the portals formed by the
second maxillipeds its course is hard to trace, but the following
seems to be its fate. If it be small in quantity and finely divided,
or very soft, it is abandoned to the action of the maxillules, by
whose strong, fringed laciniæ it is swept forwards and probably
caused to enter the mouth through the slit between the para-
gnatha. The laciniæ can be moved separately, and the difference
between them, in shape and in the kind of bristles they bear,
probably corresponds to some difference in function. If the food
be bulky or tough, the second maxillipeds assist the maxillules in
brushing it forwards towards the incisor processes. The action
of these latter is not so much a cutting as a process of tucking
the food into the lip-chamber by first backing outwards and then
moving inwards and rotating upwards. No doubt, during this
the food generally undergoes some tearing, and when the mass
of it is large, pieces have to be torn from it before they can be
swallowed. The palp does not appear to take any mechanical
part in the process of feeding. If it has a sensory function this
is probably not of great importance, for the organ is present and
absent in closely related genera in many cases among Carides.
Finally, to enter the gullet, the food must pass between the
molar processes and doubtless be pounded by them as it goes.
Their concave ends are usually found to be clogged with a pasty
matter. They must do their work very quickly, for the move-
ment of the mandibles, as judged by that of the incisor processes,
ceases very soon after the food leaves the latter. How swallowing
takes place is not clear. Parker and Mocquard suggest that the
food of Decapod crustaceans is caused to pass up the gullet by
suction from the crop (stomach), but, as I have shown elsewhere *,
the case of the land hermit-crabs of the genus *Cœnobita* throws

---

* Gardiner's 'Fauna of the Maldives,' vol. i. p. 79 (1901).

doubt upon this explanation. It may be that the constrictor muscles of the œsophagus conduct the process.

2. The first maxillipeds and the maxillæ probably take no very prominent part in manipulating the food. The feeble lobes of the maxillæ are in incessant movement to and from the middle line as they are carried inwards and outwards by the action of the scaphognathite. It seems not unlikely that their sole function is to regulate the motions of the latter. The large lacinia of the first maxilliped is a rather weak structure, with slender silky bristles, and is not strongly moved during feeding. Probably, by covering the lobes of the maxilla, it prevents them from being clogged by the food.

The part played by the paragnatha seems to be a passive one.

The labrum undergoes active movements, whose function is probably to aid in keeping the food under the action of the incisor processes.

3. The exopodites of the maxillipeds are in constant rapid motion, setting up by their activity a strong current forwards from the mouth. No doubt, this assists in carrying away the exhausted water from the gill-chambers and the excreta of the green glands poured out at the base of the antennæ. But it has also a significance in the feeding process. From time to time particles are rejected by the second maxillipeds, which kick them violently forwards, the distal parts of the third maxillipeds at the same time straightening so as to admit them to the outgoing stream, by which they are swept away.

Explanation of Lettering of the Text-figures.

1–8, endites or the primary segments which correspond to them.
9, additional segment in the maxilliped of *Calanus*.
1 *l.*, 2 *l.*, first and second lobes of maxilla of Decapoda.
1 *lg.*, first leg of *Leander*.
1 *mxp.*, 2 *mxp.*, 3 *mxp.*, first, second, and third maxillipeds of *Leander*.
ap., apical lobe.
a.r., third or additional row of setæ on thoracic limb of *Nebalia*.
ax., axis of parapodium.
bas., basipodite.
b.is., basi-ischiopodite.
b.m., base of mandible.
car., carpopodite.
cox., coxopodite.
dac., dactylopodite.
d.c., dorsal cirrus.
en., endopodite.
ep., epipodite.
ex., exopodite.
fl., flabellum.
g., gill of polychæte worm.
gl., papilla for opening of maxillary gland of Stomatopoda.
gr., groove across paragnathum of *Leander*.

i., incisor process of mandible.
i.l., inner lacinia of maxillule of Malacostraca.
isc.mir., ischio-meropodite.
l., labrum.
l.', side lobe of labrum.
l.r., lateral row of setæ.
m., molar process of mandible.
m.r., marginal row of setæ.
mer., meropodite.
n., notch on paragnathum to receive endopodite of maxillule.
o.l., outer lacinia of maxillule of Malacostraca.
p., paragnathum.
p.m., palp of mandible.
pr.cx., precoxa.
pr.ep., proepipodite.
pro., propodite.
pro.dac., pro-dactylopodite.
r., *r.'*, *r.''*, ridges of segments of first leg of *Leander*.
s.r., second side row of setæ.
s., subapical lobe.
v.c., ventral cirrus.
x., so-called " exopodite " of *Triarthrus*.